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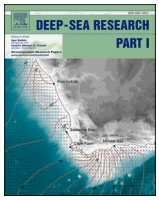

Trophic ecology and niche segregation among coexisting *Macrourus* species at South Georgia, Southern Ocean

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ABSTRACT

Despite their importance in food webs and predominance among species bycaught in Southern Ocean toothfish fisheries, the trophic ecology of grenadiers of the genus *Macrourus*, remains poorly understood. Here, we provide the first comprehensive assessment of trophic position, niche segregation and dietary composition of four *Macrourus* species: *M. caml*, *M. carinatus*, *M. holotrachys*, and *M. whitsoni*. *M. holotrachys* had the highest trophic position (highest δ^{15}N values) and the highest mean δ^{13}C values, indicative of a benthic diet; *M. caml* and *M. carinatus* had intermediate and to some extent overlapping δ^{15}N and δ^{13}C values, and the widest isotopic niches, and; *M. whitsoni*, had the lowest δ^{15}N and δ^{13}C values, indicative of a lower trophic position and more pelagic diet. These differences in stable isotope values were reflected in their feeding strategies and diets; although all four species are generalist feeders, with crustaceans and fish as their main prey, *M. holotrachys* exhibited a more specialized benthic feeding strategy (hence a higher vulnerability to bycatch), whereas *M. caml* and *M. carinatus* had broader benthopelagic diets. The niche segregation is likely shaped by depth distribution and habitat preferences, which reduces competition for prey and enables their coexistence. This study is the most comprehensive assessment to date of the trophic ecology of *Macrourus* species in the Southern Ocean, increasing our understanding of their ecological role in the deep-sea food web and providing valuable insights for their management.

1. Introduction

The Macrouridae (grenadiers) is a speciose family of deep-sea fish comprising ~375 species worldwide (Iwamoto, 2008; Fricke et al., 2026). They are abundant, mainly benthopelagic predators and scavengers, inhabiting depths ranging from the upper continental slopes (~200 m) to abyssal plains (~7000 m) (Smith et al., 2011; Fricke et al., 2026). Within the *Macrourus* genus, four species are known in the Southern Ocean: *Macrourus caml* (McMillan et al., 2012), *M. carinatus* (Günther, 1878), *M. holotrachys* (Günther, 1878) and *M. whitsoni* (Regan, 1913; Smith et al., 2011; Gon et al., 2021). *M. carinatus* and *M. holotrachys* are more abundant north of 60° S, in sub-Antarctic regions (van Wijk et al., 2003; Nowara et al., 2015; Gregory et al., 2017; Gon et al., 2021), whereas *M. caml* and *M. whitsoni* are more common

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south of the 60° S, particularly in the Ross Sea region (Pinkerton et al., 2012, 2013; Gon et al., 2021; Moore et al., 2022).

Macrourids play an important role in Southern Ocean deep-sea ecosystems as prey, predators and scavengers. They are predated and consumed in large numbers by Patagonian and Antarctic toothfish (*Dissostichus eleginoides* and *D. mawsoni*, respectively) (Pilling et al., 2001; Stevens et al., 2014; Grüss et al., 2023; Queirós et al., 2025a) and by skates (Barbini et al., 2018; Faure et al., 2023). They feed on a variety of benthic and pelagic organisms throughout their distributions (Morley et al., 2004; Laptikhovsky et al., 2014; Pinkerton et al., 2012; Münster et al., 2016; Ñacari et al., 2022). As scavengers, they influence the food web structure by redistributing energy and recycling nutrients (Drazen et al., 2001; Yau et al., 2002). These roles underscore their importance in marine food webs, where they act as crucial links between benthic and pelagic habitats (Pinkerton et al., 2012; Ñacari et al., 2022; Queirós et al., 2025a). However, few studies have assessed the trophic role and diet of macrourid species in the Southern Ocean, focusing on a single species or at higher taxonomical levels (e.g. genus) (Morley et al., 2004; Pinkerton et al., 2012, 2013).

Macrourids exhibit marked differences in key biological parameters, including growth, age structure, maturity, as well as in habitat preferences and both horizontal and vertical distributions (Moore et al., 2022; Grüss et al., 2023; Abreu et al., 2026). Accordingly, interspecific niche segregation, including in feeding strategies and prey selection, likely reduces direct competition and contributes to their coexistence in some environments (Laptikhovsky et al., 2014; Pinkerton et al., 2012; Lee et al., 2019). Macrourid species are considered to be either diet generalists or specialists (Laptikhovsky et al., 2014; Stevens et al., 2020). Generalist species tend to have wider trophic niches and are likely to be less vulnerable to changing conditions (Bond et al., 2016; Queirós et al., 2022). In contrast, the narrower trophic niche of specialist species probably makes them more vulnerable to changes in the distribution, abundance or availability of their prey (Matich et al., 2011; Bond et al., 2016).

Stomach contents are often used for studies of fish feeding ecology as they provide information on prey species, size, age and sex (Pilling et al., 2001; Pinkerton et al., 2012; Main et al., 2009; Roberts et al., 2011; Stevens et al., 2014; Queirós et al., 2022). However, they are subject to biases, including variable prey digestion rates and the potential underrepresentation of rare and easily digested items (Hyslop, 1980; Pierce and Boyle, 1991; Faure et al., 2023). Additionally, the capture methods for deep-sea species, such as longlining, often result in everted stomachs or regurgitation of stomach contents due to the expansion of gas in the swim bladder (barotrauma), further complicating analysis (Laptikhovsky, 2005; Jones, 2008; Stevens and Dunn, 2011). To overcome these limitations, trophic proxies such as stable isotopes (mainly $\delta^{13}C$ and $\delta^{15}N$) have been used as a complementary method, integrating diet over time and providing insights into trophic position and energy pathways (Newsome et al., 2007; Stowasser et al., 2009; Faure et al., 2023). Values of $\delta^{13}C$ do not vary greatly with trophic position and are commonly used to determine the dietary carbon source, providing information on habitat, with higher values generally associated with benthic-derived food webs and lower values indicating a reliance on pelagic carbon sources (McCutchan et al., 2003; Newsome et al., 2007). In contrast, consumer tissue is enriched in ^{15}N in relation to their prey, and thus $\delta^{15}N$ indicates relative trophic position (McCutchan et al., 2003; Newsome et al., 2007). The combination of stable isotope and stomach content analyses therefore allows for a more comprehensive understanding of trophic niche differentiation and feeding ecology, including in marine organisms, such as fish.

South Georgia is a subantarctic archipelago located at the north of the Scotia Sea, Southern Ocean. The surrounding waters form part of the South Georgia and South Sandwich Islands Marine Protected Area (MPA), one of the largest MPAs in the world, representing 5.2% of global marine protected area coverage (Hogg et al., 2011; Gregory and Belchier, 2026). This region supports high biodiversity and endemism, including of predators such as seabirds and marine mammals, and pelagic and deep-sea fish, all of which rely on the area for feeding and breeding (Murphy et al., 2007; Clarke et al., 2012; Stowasser et al., 2012; Morley et al., 2014; Trathan et al., 2014). At South Georgia, much more research has focused on the pelagic and shelf ecosystems than on the demersal deep-sea component (Stowasser et al., 2009, 2012; Queirós et al., 2025a). Knowledge of deep-sea food webs, including the ecological roles of species such as macrourids, is crucial for understanding wider ecosystem functioning and supporting ecosystem-based management of Southern Ocean fisheries.

The four species of *Macrourus* comprise the main bycatch in the Patagonian toothfish *D. eleginoides* longline fishery at South Georgia (Convention for the Conservation of Antarctic Marine Living Resources [CCAMLR] Subarea 48.3; CCAMLR, 2023), as well as in all other toothfish fisheries in the Southern Ocean (Abreu et al., 2026). Conservation measures limit these fisheries to depths between 700 m and 2250 m, to protect smaller and younger toothfish, yet these depths overlap with the habitats of adults of all four macrourid species (Collins et al., 2010; Abreu et al., 2024). Macrourid species may also exhibit differing vulnerability to fishing, likely related to their distribution and life-history characteristics (Morley et al., 2004; Lee et al., 2019; Moore et al., 2022). Consequently, macrourid bycatch (which are not commercialised), poses a challenge to the ecosystem-based management required under CCAMLR in the Southern Ocean (Constable et al., 2000; Trathan, 2023), particularly given the limited understanding of the trophic implications of removing these species from the deep-sea ecosystems.

Given the above context, improved baseline knowledge of biology, diet, feeding behaviour and ecological role of macrourid species in deep-sea ecosystems is vital. Here, we report on the most comprehensive study of trophic ecology of *M. caml*, *M. carinatus*, *M. holotrachys* and *M. whitsoni* in the Southern Ocean (including the four species) through stable isotope analyses and stomach contents. Our main objectives were to, i) assess interspecific differences in trophic position and carbon source, and hence ecological niches, ii) describe the diet of all four species using stomach contents, and iii) examine the implications of their feeding strategies in the context of improving ecosystem-based fishery management in Southern Ocean longline fisheries, including around South Georgia.

2. Material and methods

2.1. Data collection

Macrourus spp. were sampled during six consecutive fishing seasons (May to August in 2018 to 2023) of the Patagonian toothfish longline fishery at South Georgia (CCAMLR subarea 48.3). Macrourids were caught incidentally at depths of 700 m to 1800 m. All individuals were identified to species level, sexed, weighed (kg) and measured (total length (cm)), in accordance with the CCAMLR Scheme of International Scientific Observation (CCAMLR, 2026). Latitude, longitude, date, and depth (m) of each longline set were obtained from vessels' reporting forms (CCAMLR C2).

In total, 717 fish of the four macrourid species were examined across the six seasons; 74% (n = 527) had everted stomachs, leaving 190 non-everted stomachs suitable for diet analysis. Stable isotope analyses were limited to individuals caught in 2023 to avoid possible confounding effects of annual variation in baselines. Sample size was as follows: *M. caml*, n = 40; *M. carinatus*, n = 20; *M. holotrachys*, n = 39; *M. whitsoni*, n = 12. After identification, muscle samples were collected from the lateral body wall, near the dorsal fin, and preserved at −20 °C, either on board the fishing vessels or at King Edward Point Research Station (South Georgia) until stable isotope analysis. Fish muscle samples are considered to integrate diet over the preceding ~ 2-3 months (Buchheister and Latour, 2010; Martino et al., 2019). Sampling locations (muscle and stomachs samples) were distributed around South Georgia,

with substantial spatial overlap among the four macrourid species (Fig. 1). Individuals examined for stable isotope analyses and stomach contents spanned a major proportion of the length distribution observed in the longline bycatch, and thus were broadly representative (Figs. S1 and S2).

2.2. Stable isotope analysis

Muscle samples were lyophilized for a minimum of 36 h, dried and powdered before extracting lipids using cyclohexane (C_6H_{12}). Since lipids are depleted in ^{13}C compared to proteins, lipid content can affect the relative abundance of ^{13}C in consumer tissues (Post et al., 2007; Hussey et al., 2012). After delipidation, samples were dried overnight in an oven at 45 °C. C/N ratios clustered narrowly around 3.1 (Table S1), indicating successful removal of the lipids. Between 0.2 and 0.4 mg of sample were weighed into a tin capsule using a Mettler Toledo® XPR6UD5 microbalance. Isotope values of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were determined with a Continuous Flow Mass Spectrometer (Thermo Scientific® Delta V Plus – Isotope Ratio Mass Spectrometer) coupled with an elemental analyser (Thermo Scientific® Flash, 2000). Results are reported in δ notation and expressed as parts per thousand, relative to international standards (Vienna-Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen). C:N mass ratios were determined from percentage element weights. Values were normalised using USGS-61 and USGS-63 (Caffeine, United States Geological Survey) as reference materials. Replicate measurements of reference materials throughout the analyses showed an uncertainty <0.10 ‰ for $\delta^{13}C$ and <0.14 ‰ for $\delta^{15}N$ for all sample runs. Stable isotopic analyses were performed at the Littoral, Environment and Societies (LIENSs) laboratory at the University of La Rochelle, France.

2.3. Stomach content analysis

In the laboratory, stomachs were thawed, weighed and opened in a fine sieve. Prey items were identified to the lowest taxonomic level using published identification guides: Gon and Heemstra (1990) and Reid (1996) for fish, Xavier et al. (2020) for crustaceans, and Xavier and Cherel (2021) for cephalopods, along with reference collections at King Edward Point Research Station (South Georgia) and at Marine Environmental Science Centre (MARE-UC) (Coimbra). If present, occasional parasites, small stones and bait were weighed but excluded from further analysis. For each stomach, all prey in each taxon were counted and weighed (nearest 0.01 g).

The relative importance of different prey in the diet of the four macrourid species was compared using the Index of Relative Importance (% IRI) (Cortes, 1997). IRI was calculated using the formula $IRI = \%O\ (\%N + \%M)$ where $\%O$ is the percentage occurrence by diet sample, $\%N$ is the percentage by prey number (numerical abundance) and $\%M$ is the percentage wet mass in stomachs. The IRI does not have a set scale and hence was converted to percentage (%IRI): $\%IRI = (IRI/\sum IRI) \times 10^2$ (Cortes, 1997; Bethea et al., 2007) to allow comparison with previous studies. To simplify the dietary data, correct for uneven taxonomic resolution, and facilitate comparisons, prey items were classified into eight broad categories: Cephalopods, Cnidarians, Crustaceans, Echinoderms, Fish, Polychaetes, Sponges, and unknown.

Cumulative prey-species curves, i.e., plots of the prey species richness against the number of stomachs with identifiable prey, were used to check if enough samples had been collected to accurately describe the diet of each species (Cortes, 1997). Curves were generated after 1000 randomizations of the original data using the *specaccum* function (method: random, permutations: 1000) from the *vegan: Community Ecology* package (Oksanen et al., 2020). When the curves approached an asymptote, it is considered that enough stomachs were sampled to accurately characterise the diet.

2.4. Data analysis

All statistical tests were performed considering $\alpha = 0.05$. The distributions of $\delta^{13}C$, $\delta^{15}N$ values and total length data were assessed for normality using the Shapiro–Wilk test, and for homogeneity of variances with Bartlett's test. Sex-specific differences in $\delta^{13}C$ and $\delta^{15}N$ values were assessed by species using a student *t*-test when assumptions of normality and equal variance were met, or a Mann–Whitney *U* test otherwise. Inter-specific differences in $\delta^{13}C$, $\delta^{15}N$ values and total length were tested by one-way ANOVA followed, when significant, by Tukey's multiple-comparison test. The relationships between isotopic signatures and total length for each species were tested by fitting a generalized linear model (GLM) using $\delta^{13}C$ and $\delta^{15}N$ as response variable, and species, total length and their interaction as explanatory variables. Fitted relationship were visualised with the *effects* and *ggplot2* packages. Model

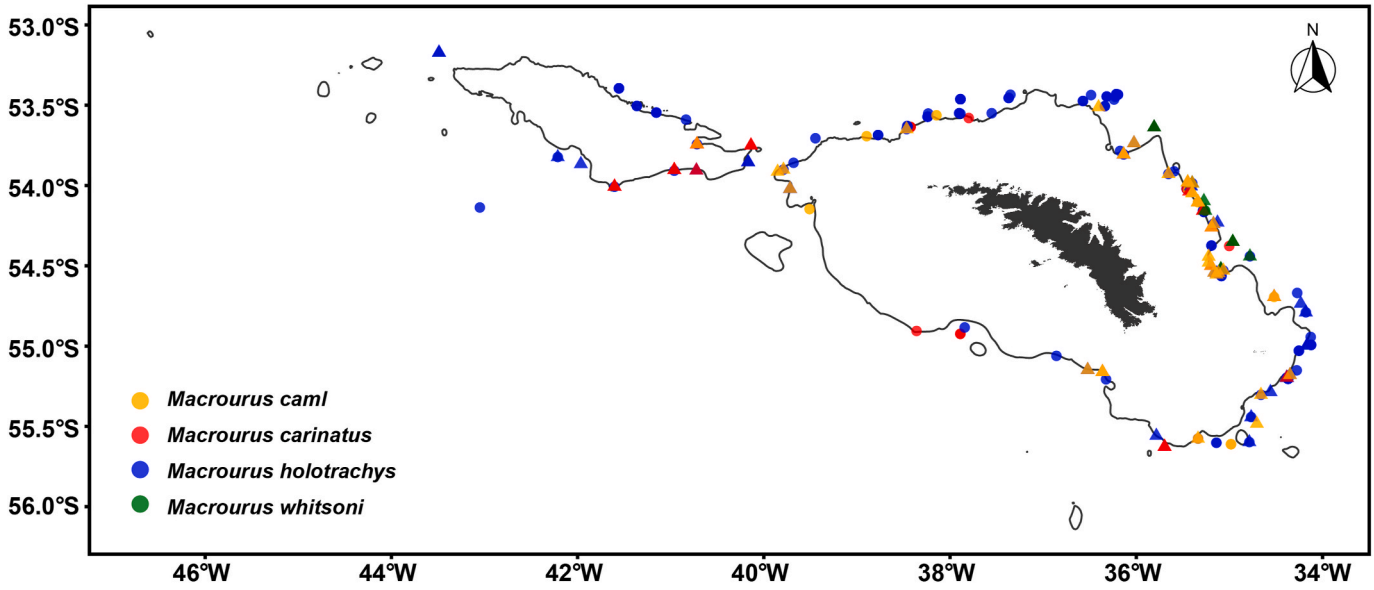

Fig. 1. Sampling locations of the four macrourid species collected around South Georgia (CCAMLR subarea 48.3). Circles indicate stomach-content samples and triangles indicate muscle samples used for stable isotope analyses, with colours representing each species. The black line denotes the 1000 m bathymetric contour. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

assumptions of linearity, homoscedasticity and normality of residuals were verified using the *performance* package (Lüdecke et al., 2021). Bayesian standard-ellipse areas corrected for small sample size (SEAc) and species overlap, were computed using the *SIBER* package (Jackson et al., 2011), to compare isotopic niche width, and standard ellipse areas plotted for visualization of the data. All data visualization, statistical exploration and analyses were carried out in R environment v4.3.1. (R Core Team, 2023).

3. Results

3.1. $\delta^{13}C$ and $\delta^{15}N$ values of macrourid species

Stable isotope values varied significantly among the four macrourid species, with differences found for both $\delta^{13}C$ (ANOVA: $F = 14.69$, $p < 0.001$) and $\delta^{15}N$ (ANOVA: $F = 83.54$, $p < 0.001$) (Fig. 2; Table S1). Values for $\delta^{13}C$ were highest in *M. holotrachys* and intermediate in *M. caml* and *M. carinatus*, although with a wide range in the latter species such that there was no significant difference from *M. whitsoni*, which had the lowest values (Fig. 2; Table S1). The pattern in $\delta^{15}N$ was broadly similar, with significantly higher values in *M. holotrachys*, intermediate values in *M. caml* and *M. carinatus*, with no significant difference between these two species, and lowest values in *M. whitsoni* (Fig. 2; Table S1). There were no significant differences in either $\delta^{13}C$ or $\delta^{15}N$ values between males and females of the four species (two-sample *t*-tests/Mann–Whitney U tests; $p > 0.05$; Table S2).

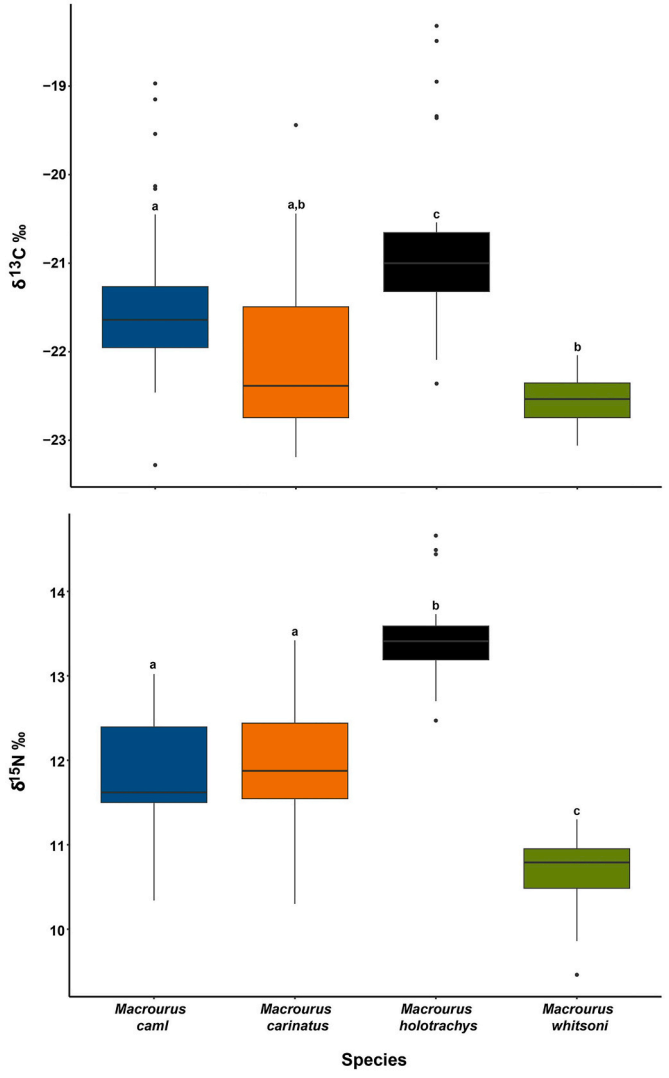

Fig. 2. Box-plots of $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) values (‰) for the four macrourid species collected at South Georgia (CCAMLR Sub-area 48.3). Boxes represent the middle 50% of the data with a median line; whiskers extend to the most extreme non-outlier values, and black points denote outliers. Species sharing a superscript letter do not differ significantly.

M. holotrachys showed a significant positive relationship between $\delta^{13}C$ values and total length ($p = 0.016$; Table 1; Fig. 3a). At comparable lengths, *M. holotrachys* muscle was significantly more enriched in ^{13}C than the other macrourid species, particularly *M. carinatus* ($p < 0.001$), and possibly more enriched in ^{13}C than *M. whitsoni*, although the test was inconclusive due to low sample size and limited statistical power (Table 1). Although the slope of the relationship in *M. caml* differed significantly from that of *M. holotrachys* ($p = 0.022$; Table 1), it was not significantly different from zero and was the only negative slope among the macrourid species (Fig. 3a). Likewise, the linear relationships between length and $\delta^{13}C$ values for *M. carinatus* and *M. whitsoni* were not significant (Table 1). In contrast, $\delta^{15}N$ values differed significantly among species but there was no clear evidence of a change with body length (Table 1; Fig. 3b). At comparable lengths, *M. holotrachys* exhibited significantly higher $\delta^{15}N$ values than all other macrourid species (all $p < 0.001$). Although $\delta^{15}N$ values tended to increase with total length within each species, the trends were not significant (all $p > 0.05$) (Fig. 3b; Table 1). However, if data were pooled across species, $\delta^{15}N$ increased significantly with total length ($p < 0.001$), revealing a positive overall length–trophic position relationship at genus level.

A comparison of Bayesian standard ellipses indicated that the four macrourid species differed in their isotopic niche (Fig. 4). The niche area was broadest in *M. carinatus* (SEAc = 2.25 ‰^{2}), and narrowest in *M. whitsoni* (0.50 ‰^{2}). The extensive ellipse of *M. carinatus* mirrored its wide range in $\delta^{13}C$ values. In contrast, the compact ellipse of *M. whitsoni* was based on the low $\delta^{13}C$ and $\delta^{15}N$ values, and indicated a low trophic position. *M. caml* (SEAc = 1.27 ‰^{2}) and *M. holotrachys* (1.09 ‰^{2}) displayed similar niche sizes but divergent positions: the niche of *M. caml* was offset toward lower $\delta^{13}C$, whereas that of *M. holotrachys* reflected higher $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 4). The ellipses of *M. caml* and *M. carinatus* overlapped substantially (52% of *M. caml* niche), reflecting their shared median isotopic values and hence potentially similar trophic positions, whereas overlap among all other species-pairs was negligible (<3%).

3.2. Stomach contents composition and species comparison

A total of 190 non-everted macrourid stomachs were examined, including *M. caml* (n = 33), *M. carinatus* (n = 21), *M. holotrachys* (n = 135) and *M. whitsoni* (n = 1) (Table S3). A large proportion of these were empty, and so the total number of stomachs available for diet analyses was 9, 8, 104 and 1, for *M. caml*, *M. carinatus*, *M. holotrachys* and *M. whitsoni*, respectively.

In total, 298 prey items were found in the stomachs of the four macrourid species, including crustaceans (n = 204; 68%), fish (n = 44; 15%), Cephalopoda (n = 7; 2%), Polychaeta (n = 7; 2%), Echinodermata (n = 6; 2%), Cnidaria (n = 2; <1%), Porifera (n = 1; <1%), and unidentified (n = 27; 9%) (Table 2). Crustaceans and fishes collectively accounted for >75% of the total IRI in every macrourid species. Considering each species individually, the most important prey category in terms of %IRI was crustaceans for *M. holotrachys* (82%), *M. carinatus* (73%) and *M. whitsoni* (52%), and fish for *M. caml* (68%) (Table 2). All other prey categories occurred only sporadically, e.g., cephalopods were present exclusively in *M. caml* and *M. holotrachys*. The %IRI of unidentified prey items ranged from 3% in *M. holotrachys* to 17% in *M. carinatus* (Table 2).

Cumulative prey-species curves indicate there were differences in sampling coverage among species (Fig. 5). The curve for *M. holotrachys*, which had the largest sample size (n = 104), reached 28 identifiable prey species towards an asymptote, with the final ten stomachs

Table 1
Results of the Generalized Linear Models (GLM) for δ^{13}C and δ^{15}N values of the four macrourid species collected at South Georgia (CCAMLR subarea 48.3). *Macrourus holotrachys* was used as reference species. Significant effects ($p < 0.05$) are highlighted in bold.

Coefficient		Estimate	St. Error	t-value	p value	Deviance			
						Residual	df	Null	df
δ^{13}C (‰)	Intercept	−20.932	0.139	−150.093	**<0.001**	74.696	103	115.226	110
	M. caml	−0.549	0.194	−2.824	**<0.010**				
	M. carinatus	−1.285	0.277	−4.632	**<0.001**				
	M. whitsoni	−1.180	0.738	−1.598	0.113				
	Length	0.035	0.014	2.447	**0.016**				
	M. caml:length	−0.049	0.021	−2.322	**0.022**				
	M. carinatus:length	−0.004	0.025	−0.147	0.883				
	M. whitsoni:length	−0.008	0.046	−0.167	0.867				
	AIC = 289.04								
δ^{15}N (‰)	Intercept	13.371	0.101	132.715	**<0.001**	38.984	103	135.897	110
	M. caml	−1.621	0.140	−11.543	**<0.001**				
	M. carinatus	−1.459	0.200	−7.281	**<0.001**				
	M. whitsoni	−2.555	0.533	−4.790	**<0.001**				
	Length	0.014	0.010	1.401	0.164				
	M. caml:length	0.002	0.015	0.117	0.907				
	M. carinatus:length	−0.006	0.018	−0.354	0.724				
	M. whitsoni:length	−0.003	0.033	−0.077	0.939				
	AIC = 216.86								

contributing <3% greater richness (Fig. 5). In contrast, the cumulative prey-species curves for *M. caml* and *M. carinatus* remained far below an asymptote (Fig. 5). For *M. whitsoni*, a cumulative prey-species curve could not be constructed as there was only one stomach sample.

4. Discussion

Considerably less is known about the trophic ecology and population dynamics of bycatch than target species in commercial fisheries (Norse et al., 2012; Gray and Kennelly, 2018). This is particularly true for deep-sea species in the remote Southern Ocean (Chown et al., 2022; Constable et al., 2023). Here, we present the first comparative study of the trophic ecology of the four macrourid species at South Georgia, which together constitute the majority of bycatch in Southern Ocean longline fisheries. *M. holotrachys* occupied the highest trophic position, and based on δ^{13}C values and stomach contents, consumed more benthic prey, whereas the other three macrourid species had a more benthopelagic diet. In addition, our results indicated that isotopic niches of *M. caml* and *M. carinatus* overlapped and were broader than, and distinct from, those of *M. holotrachys* and *M. whitsoni*. Crustaceans were the most important prey, followed by fish in three of the four species. The exception was *M. caml*, which consumed more fish than crustaceans. *M. holotrachys* fed more on benthic invertebrates, whereas *M. caml* seemed to rely more on pelagic prey. However, limited sample size precluded a complete assessment of their diet (see section 4.4). Regardless, our results indicate there is clear niche segregation among the four macrourid species in the benthopelagic ecosystem at South Georgia.

4.1. Trophic niches

Comparison of δ^{13}C and δ^{15}N values revealed clear trophic differences among species. *M. caml* and *M. carinatus* exhibited substantial overlap in isotopic niches, suggesting that a proportion of individuals occupy similar habitats. However, their dietary preferences (discussed below) suggest they may occupy slightly different roles within their shared habitat (also see Fitzcharles, 2014). Their δ^{13}C values indicate a benthopelagic diet, and cover a wide range, which corroborates previous conclusions that both these species have the most generalist diet and occupy the widest depth range of the four macrourid species (Laptikhovsky, 2005; Pinkerton et al., 2012; Abreu et al., 2026). The correlation between size and δ^{13}C values in *M. caml* suggested that its broad niche is partly related to an ontogenetic shift towards pelagic habitats as adults.

In contrast, *M. holotrachys* occupied the highest trophic position, reflecting its predatory role in benthic food webs (Laptikhovsky, 2005; Boyle et al., 2012). Queirós et al. (2025a) found similar results; *M. holotrachys* exhibited higher δ^{15}N values than the Patagonian toothfish, usually considered the top fish predator at South Georgia (Collins et al., 2010). Studies in different marine ecosystems across the Southern, Atlantic and Pacific oceans have shown enrichment in ^{15}N and ^{13}C in benthic compared with pelagic food webs (Drazen et al., 2008; Boyle et al., 2012; Amiraux et al., 2023). This was also observed in our study, as the larger *M. holotrachys* had higher δ^{13}C values, suggesting a progressive shift towards carbon sources associated with benthic pathways, and more specialized feeding behaviour. High δ^{15}N values may also suggest greater reliance on scavenging (Yau et al., 2002; Laptikhovsky, 2005; Ñacari et al., 2022), making this species more susceptible to bycatch on longlines.

M. whitsoni had the lowest mean δ^{15}N and δ^{13}C values, indicative of a lower trophic position and more pelagic feeding strategy. It is also the smallest of the four species recorded at South Georgia (see Abreu et al., 2026) and exhibits several characteristics consistent with a range-edge population, including a more confined spatial distribution, lower abundance relative to central populations, greater temporal variability, and potentially reduced growth efficiency (Sexton et al., 2009). These may serve to minimise competition with its larger congeners. In contrast, in the Ross Sea where it is one of the dominant macrourid species and attains larger sizes, both its niche and diet seem to be much broader (Pinkerton et al., 2012; Moore et al., 2022). Similarly, in the South Sandwich Islands, this species also reaches large sizes and, based on comparison of stable isotope ratios, feeds ~0.3 trophic levels above the individuals we sampled at South Georgia (Queirós et al., 2025b).

The relationship between δ^{15}N values and total length in the four macrourid species were not significant but probably reflect the narrower size ranges (as individuals are all adults) and reduced statistical power because of the small sample sizes (Pinkerton et al., 2012; Münster et al., 2016). The relationship across species likely reflects the combination of possible ontogenetic shifts and inter-specific differences in size. This corroborates results from previous studies which showed that larger macrourid individuals tend to feed on larger prey and slightly higher in the food web (Loutrage et al., 2024; Baeck and Chung, 2025).

The largely distinct isotopic niches and feeding strategies exhibited by the four macrourid species reinforce their interspecific segregation at

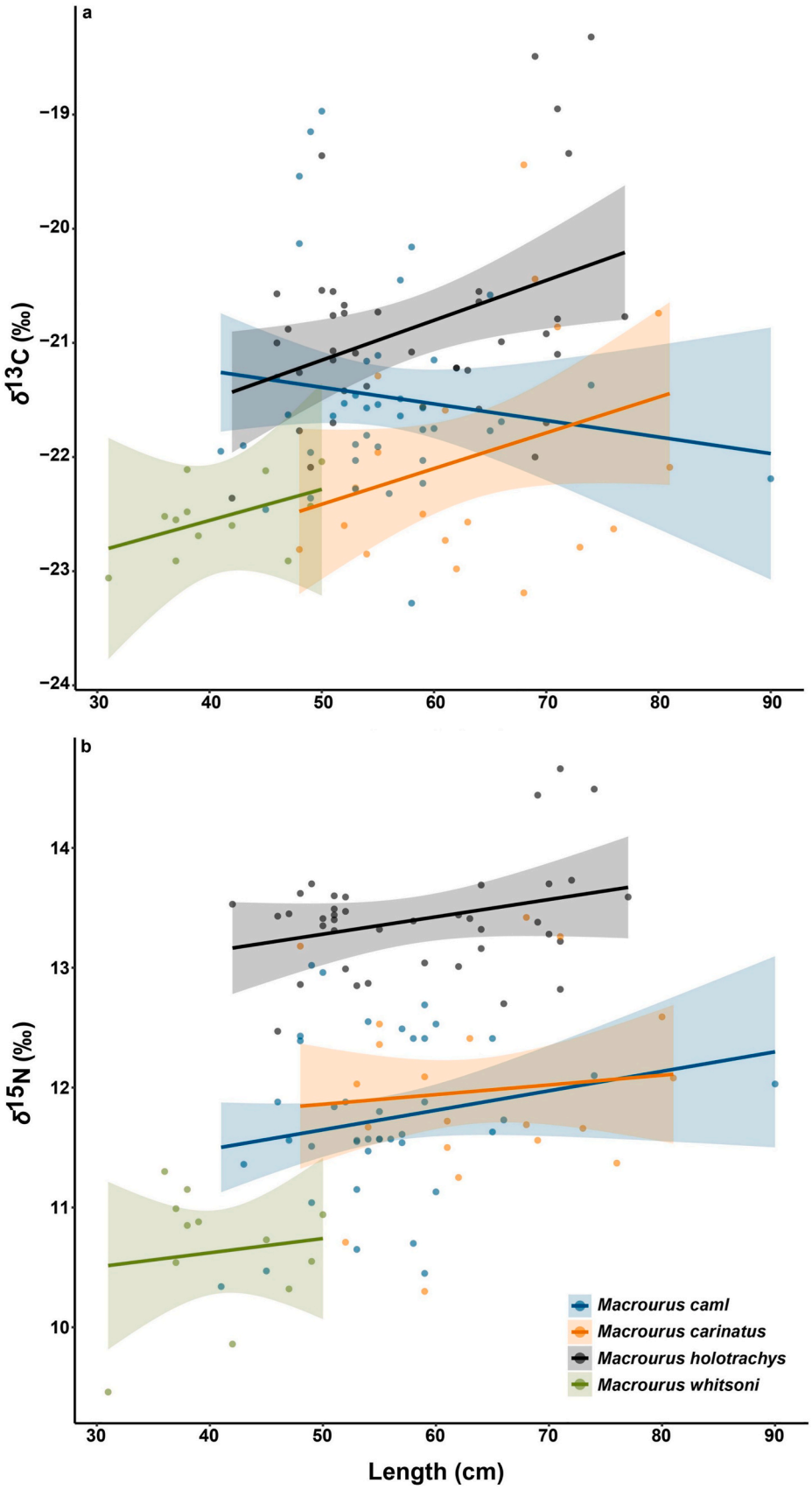

Fig. 3. Relationship between (a) δ^{13}C, (b) δ^{15}N values (‰) and total length (cm) for the four macrourid species collected at South Georgia (CCAMLR subarea 48.3). Lines represent species-specific predictions from the GLM. Shaded bands indicate 95% confidence intervals.

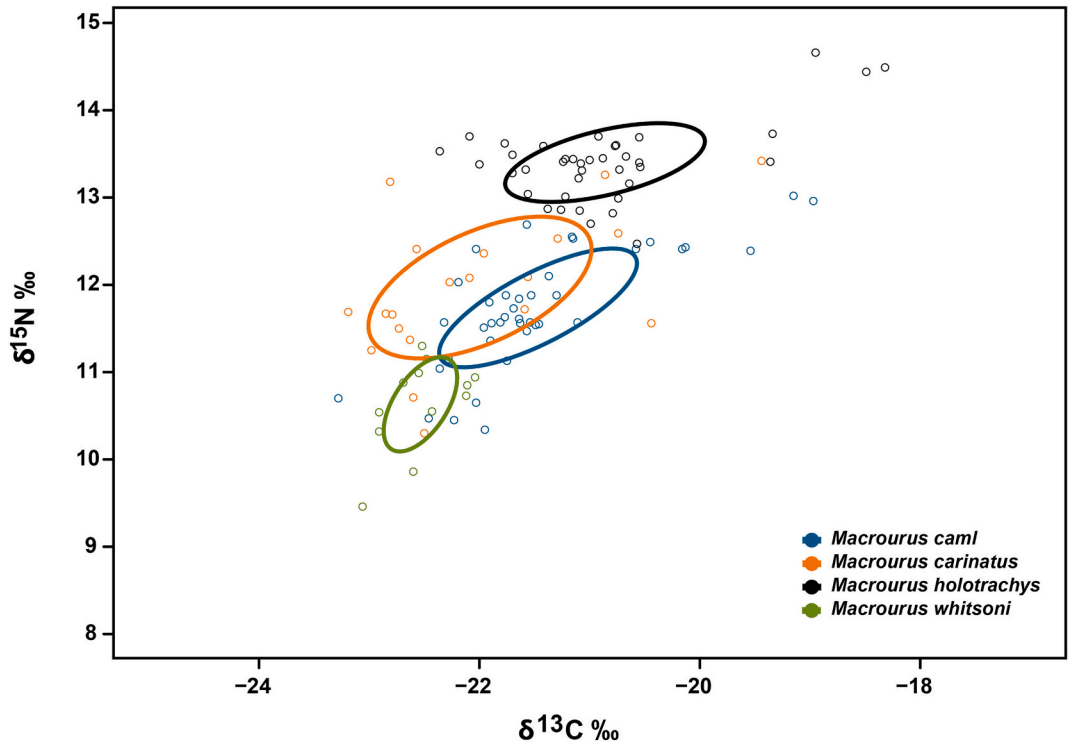

Fig. 4. Isotopic niches of the four macrourid species collected at South Georgia (CCAMLR subarea 48.3). Coloured points represent individual stable isotope values of each species, respectively. Solid lines denote the SEA_C (40%), which represents the amount of isotopic space filled by each species, reflecting both trophic status and habitat use simultaneously.

South Georgia, though with some overlap in *M. caml* and *M. carinatus*. The pattern is likely similar in other regions where these species co-occur (Dell et al., 2015; Gon et al., 2021). The depth distribution and spatial segregation of macrourid species at South Georgia (Abreu et al., 2026) are likely key factors in reducing competition for prey. As such, these different feeding strategies, shaped also by depth and habitat distribution, likely enable coexistence of the four species at South Georgia.

4.2. Interspecific comparison of diets

The dietary composition of *M. caml*, *M. carinatus* and *M. holotrachys* at South Georgia is consistent with previous studies that indicated that macrourids are generalist predators, and likely opportunistic scavengers, feeding on crustaceans, mesopelagic and benthic fish, cephalopods, echinoderms, polychaetes and, occasionally, crustacean egg masses (Drazen et al., 2001; Morley et al., 2004; Laptikhovsky et al., 2014; Pinkerton et al., 2012; Stevens et al., 2020). The diversity of prey indicates that macrourids are versatile and opportunistic consumers within the South Georgia marine ecosystem. Although they mostly consumed fish and crustaceans, the proportions of these and other prey groups diverged considerably, reflecting distinct feeding strategies. Unequal rates of digestion of different prey groups can lead to biases in representation within predator stomachs (Morley and Belchier, 2002; Stevens et al., 2020). Crustaceans, which are harder to digest than fish (except the otoliths), and other taxa with hard remains, may be over-represented, whereas soft-bodied prey such as polychaetes, cnidaria, and others, are often underrepresented (Bowman, 1986; Boyle et al., 2012; Faure et al., 2023). Hard structures, such as cephalopod beaks, and fish otoliths, resist digestion better than softer body parts (Xavier et al., 2022; Queirós et al., 2024). Beaks, but not mantle or other soft tissues (e.g. digestive gland), from the squid species *Slosarczykovia circumantarctica* or *Mastigoteuthis psychrophila* were identified in stomachs of *M. caml*.

Although our data on stomach contents suggest that at least three (*M. caml*, *M. carinatus* and *M. holotrachys*) of the four macrourid species, consume a wide range of prey, their feeding strategies ranged from specialized to generalist (Table 2). Sample sizes were small but both *M. caml* and *M. carinatus* displayed a broad prey spectrum, which is supported by their larger isotopic niches. Hence, it may reflect a more flexible, benthopelagic feeding strategy, consistent with diet studies in the Ross Sea and Patagonian Shelf regions (Laptikhovsky, 2005; Pinkerton et al., 2012). *M. caml* showed a stronger reliance on pelagic fish and decapods (including *Thymops* sp.) in particular, as well in some cephalopods, whereas *M. carinatus* diet included amphipods, euphausiids, and fish. Notably, the contribution of echinoderms and ophiuroids may suggest opportunistic feeding behaviour (Laptikhovsky, 2005). Such a diverse range of prey corroborates that *M. carinatus* has the largest niche. Although both *M. caml* and *M. carinatus* fed on crustaceans, those consumed by *M. caml* were mainly benthic (e.g. *Thymops* sp.), and those by *M. carinatus* were more pelagic (e.g. Euphausiidae) (Xavier et al., 2020), consistent with their respective $\delta^{13}C$ values.

In contrast, *M. holotrachys* exhibited a more specialized feeding strategy, relying mainly on benthic crustaceans, particularly amphipods, and less so on fish (Laptikhovsky, 2005; Ñacari et al., 2022; Queirós et al., 2025a). Of the few fish prey, *Muraenolepis* sp. was the most important, representing ~14% of the prey mass (Table 2). This taxon occurs across similar depth range, and it is also considered a benthopelagic forager (Fitzcharles, 2014), supporting the association of *M. holotrachys* with a benthic food web. Moreover, the occurrence of *Paralomis* sp. and polychaetes in the diet of *M. holotrachys* and not the other taxa, underscores that this macrourid specializes on benthic prey (Collins et al., 2002), corroborating the higher $\delta^{15}N$ and $\delta^{13}C$ values observed.

As only one stomach was analysed from *M. whitsoni*, it is not possible to draw any conclusions on its diet. The small size of *M. whitsoni* at South Georgia (Abreu et al., 2026) probably make this species more susceptible to barotrauma, limiting sample sizes for diet studies (see also

Table 2
Diet of the four macrourid species collected at South Georgia (CCAMLR subarea 48.3). %O: percentage occurrence, %N: percentage by number; %M: percentage by mass; %IRI: Index of Relative Importance. Values in bold are for the prey category.

Prey species	*Macrourus caml* (n = 9)				*Macrourus carinatus* (n = 8)				*Macrourus holotrachys* (n = 104)				*Macrourus whitsoni* (n = 1)			
	%O	%N	%M	%IRI	%O	%N	%M	%IRI	%O	%N	%M	%IRI	%O	%N	%M	%IRI
Crustacea	**33.3**	**21.4**	**12.5**	**16.5**	**87.5**	**58.8**	**31.9**	**73.2**	**73.1**	**71.7**	**40.8**	**82.0**	**100**	**50**	**54.1**	**52.1**
Cheirimedon femoratus					12.5	23.5	0.8	6.7	9.6	8.7	0.3	3.1				
Decapoda	11.1	7.1	5.9	2.6					6.7	2.6	2.7	1.3				
Euphausia crystallorophias									1	0.4	<0.1	<0.1				
Euphausia superba									1.9	0.8	0.6	0.1				
Euphausiidae					12.5	5.9	7.6	3.7								
Eurythenes sp.									18.3	9.4	3.7	8.5				
Gammaridea	11.1	7.1	0.7	1.6	25	11.8	4.4	8.8	21.2	16.2	4.3	15.3				
Isopoda									14.4	6.8	3.8	5.4				
Nematocarcinus lanceopes					12.5	5.9	4.7	2.9	3.9	1.5	2.1	0.5				
Paralomis formosa									0.9	0.4	1	0.1				
Pasiphaea scotiae									3.9	1.5	4	0.7				
Pseudorchomene sp.									1	0.4	0.1	<0.1				
Thymops sp.	11.1	7.1	6	2.6					9.6	3.8	10	4.7				
Vibilia spp.									1	0.4	0.1	<0.1				
Unknown crustacea					25	11.8	14.3	14.3	26	18.9	8.2	24.8	100	50	54.1	52.1
Fish	**44.4**	**42.9**	**62.4**	**68**	**25**	**11.8**	**15.2**	**6.2**	**26.9**	**13.2**	**39.5**	**14.1**	**100**	**50**	**45.9**	**48**
Bathydraco spp.									2.9	1.1	2.2	0.3				
Bathylagidae									1.9	0.8	3	0.3				
Liparididae	11.1	7.1	8.8	3.2												
Muraenolepis sp.									4.8	2.6	13.5	2.7				
Myctophidae									1	0.4	1	0.1				
Unknown fish	44.4	35.7	53.6	71	25	11.8	15.2	14.8	20.2	8.3	19.8	20	100	50	45.9	47.9
Cephalopods	**11.1**	**7.1**	**0.1**	**1.2**					**5.8**	**2.3**	**9.4**	**0.7**				
Mastigoteuthis psychrophila									1	0.4	1	0.1				
Moroteuthopsis longimana									1.9	0.8	6.7	0.5				
Slosarczykovia circumantarctica	11.1	7.1	0.1	1.4												
Unknown cephalopod									2.9	1.1	1.7	0.3				
Echinodermata	**11.1**	**7.1**	**1.1**	**1.3**	**12.5**	**5.9**	**28.3**	**3.9**	**3.9**	**1.5**	**1**	**0.1**				
Ophiuridae					12.5	5.9	28.3	9.3	1.9	0.8	0.5	0.1				
Unknown echinodermata	11.1	7.1	1.1	1.6					1.9	0.8	0.5	0.1				
Polychaeta									**6.7**	**2.6**	**2.2**	**0.3**				
Porifera									**1**	**0.4**	**1.1**	**< 0.1**				
Cnidaria	**11.1**	**7.1**	**2.8**	**1.6**					**1**	**0.4**	**0.1**	**< 0.1**				
Unknown	**22.2**	**14.3**	**21.2**	**11.5**	**37.5**	**23.5**	**24.6**	**16.7**	**20.2**	**7.9**	**5.9**	**2.8**				

Münster et al., 2016). However, valuable insights into its feeding ecology were gained from the much larger sample size of the stable isotope analysis.

4.3. Implications for management of bycatch fish species

From a fisheries management perspective, the high bycatch rates of *M. holotrachys* in the longline fisheries at South Georgia (Morley et al., 2004; Abreu et al., 2026) could, to some extent, be explained by its feeding behaviour, abundance and overlap of the depth range with Patagonian toothfish (Morley et al., 2004; Fitzcharles, 2014). Thus, *M. holotrachys* may be more attracted to the bait used in longline fishing, increasing its bycatch rate (Yau et al., 2002; Fitzcharles, 2014; Faure et al., 2023). Its benthic foraging behaviour likely results in higher exposure to fishing gear, compared to the other macrourid species (Fenaughty, 2008; Laptikhovsky et al., 2014). Similar mechanisms may also contribute to patterns observed in other sub-Antarctic regions, such as Kerguelen, Prince Edward and Heard Island and McDonald Islands, where *M. holotrachys* is commonly the most frequently bycaught macrourid species (CCAMLR, 2026a, b, c). Comparable patterns may also occur in Chilean and Falkland toothfish fisheries, although more accurate species-specific bycatch data from these regions are needed to confirm this hypothesis (Laptikhovsky, 2005; Ñacari et al., 2022, 2023). Moreover, the energetic costs associated with reproduction might vary between males and females, potentially affecting their feeding behaviour and mortality risk (Lee et al., 2019; Moore et al., 2022). This could explain the female sex bias in bycatch observed in some macrourids (Abreu et al., 2026). Further research on sex-specific feeding rates and associated risks would be valuable in improving our understanding of these factors.

As macrourids are likely among the most abundant species in the South Georgia benthopelagic food web (Morley et al., 2004; Fitzcharles, 2014; Hollyman et al., 2022; Abreu et al., 2026), any changes in their population sizes, sex ratios, age or size structure could have major implications for the broader deep-sea ecosystem, including effects on predator-prey interactions with Patagonian toothfish. These complex species interactions and habitat relationships underscore the need for continued research and monitoring of macrourids and other key bycatch taxa in the Southern Ocean longline fishery (CCAMLR, 2023). Such information is vital to ecosystem-based fisheries management, as the ecological consequences of bycatch cannot be assessed solely through catch characteristics, but also require understanding the trophic roles, vulnerability and functional importance of affected species. In this context, species-specific trophic studies such as ours can contribute to improved ecosystem models, bycatch assessments, and more effective mitigation measures. In doing so, it will support the sustainability aims of both CCAMLR (Article II) and Marine Stewardship Council (Principle 2), which require fisheries to minimise impacts on associated and dependent species.

4.4. Limitations and future research

Our analyses were limited to some extent by the sampling constraints inherent to studies on deep-sea species. Although the longline fishery provides whole animals, it is not ideal for conventional diet studies, as it mostly leads to everted stomachs or regurgitated contents, which can bias results (Bowman, 1986; Pilling et al., 2001; Laptikhovsky, 2005; Boyle et al., 2012). For example, the single stomach sample from *M. whitsoni* limited our ability to draw conclusions regarding its diet. Based on our results, and accumulation curves (Fig. 5), to obtain a more

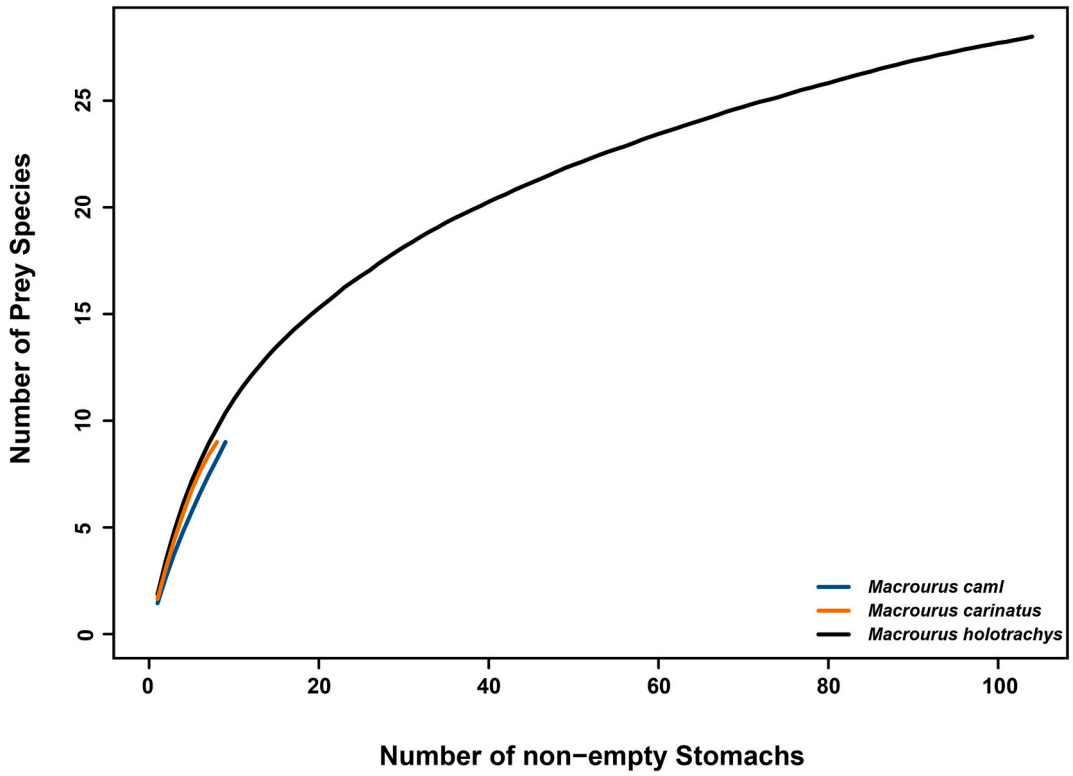

Fig. 5. Accumulation curves for the identification of new prey species in terms of number of stomachs with identifiable remains, of *Macrourus caml*, *M. carinatus* and *M. holotrachys*.

accurate representation of their diverse and generalist feeding strategies, we recommend increasing the sample size to at least 150–200 non-empty stomachs (across different depths), corresponding to a starting sample of >1000 individuals of each species, considering the likelihood of everted stomachs (Laptikhovsky, 2005).

Furthermore, seasonal variability in feeding habits is often overlooked in deep-sea species studies. For instance, it is thought that Patagonian toothfish reproduces during the fishing season, and so many of the stomachs of captured fish are empty (Bamford et al., 2024; Queirós et al., 2024). In addition, ontogenetic shifts in depth and diet are very likely to occur across all four species but may not be detected here due to fishing gear selectivity and depth restrictions. Seasonal oceanographic variability may further influence prey availability, potentially altering diet depending on depth and habitat (Laptikhovsky, 2005; Moore et al., 2022). Understanding seasonal shifts could provide valuable insights into the contribution of reproductive cycles or changes in prey abundance to dietary fluctuations.

Future studies could benefit from complementary sampling methods, such as analyses of fish caught in trawl surveys (van Wijk et al., 2003; Münster et al., 2016; Grüss et al., 2023), or DNA diet metabarcoding, which provides high taxonomic resolution allowing identification of soft-bodied or very digested prey (Faure et al., 2023; Vasiliadis et al., 2023).

Data statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

CRediT authorship contribution statement

José Abreu: Conceptualization, Formal analysis, Funding acquisition, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Richard A. Phillips:** Conceptualization, Methodology, Supervision, Validation, Writing – review & editing. **Philip R. Hollyman:** Conceptualization, Methodology, Supervision, Validation, Writing – review & editing. **José P. Queirós:** Methodology, Writing – review & editing. **Paco Bustamante:** Methodology, Writing – review & editing. **Mark Belchier:** Methodology, Writing – review & editing. **Martin A. Collins:** Conceptualization, Methodology, Supervision, Validation, Writing – review & editing. **José C. Xavier:** Conceptualization, Methodology, Supervision, Validation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2026.104733.

Data availability

Data will be made available on request.

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